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REPRODUCTION IN THE APHIDIDÆ WITH A CONSIDERATION OF THE MODIFYING INFLUENCE OF ENVIRONMENTAL FACTORS.¹

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Literature on aphids abounds in references to the existence of an "asexual" and a "sexual" reproduction. As a matter of fact, however, they reproduce sexually only, the term "sexual reproduction" being generally accepted by zoölogists as meaning reproduction by means of special reproductive cells, and "asexual reproduction" that method which involves a direct division, or budding, of an animal without the intercession of specific germ cells.

Reproduction in aphids may be subdivided into two categories: 1. *Amphigony*. This involves the union of reproductive cells of both sexes, the female gamete, or egg, necessitating fertilization by the male gamete, or spermatozoön, as a prerequisite to development. 2. *Parthenogenesis*. In this mode of reproduction the male gametes are dispensed with, the egg developing without having been previously fertilized. Hertwig and Kingsley (1912, p. 130) characterize parthenogenesis as "a sexual reproduction in which a degeneration of fertilization has taken place." In addition to the two foregoing methods of reproduction, occasional cases of *pædogensis* (e. g., in *Aphis avenæ* Fabricius, as reported by Ewing, 1916, and in *Toxoptera graminum* Rondani, Webster and Phillips, 1912) have been reported. Pædogensis is parthenogenesis occurring in the preadult stages of animals.

Amphigonous reproduction is considered as the more primitive method in insects, parthenogenesis being the result of a later specialization. The latter method of reproduction has become of normal occurrence in aphids and has practically supplanted the former, amphigony taking place only under the influence of adverse conditions in the environment. We have thus in aphids a

¹ Contribution from the Entomological Laboratories of the Bussey Institution, Harvard University. No. 191.

very remarkable instance of a highly specialized group of sexually reproducing animals in which fertilization of the female reproductive cells as a prelude to development has been reduced to an apparently unnecessary and unessential physiological process.

GENERAL FEATURES OF AMPHIGONY IN APHIDS.

In the amphigonous generation both sexes are, of course, represented. The presence of the male is the only characteristic of the amphigonous generation.

The main external characteristics of an amphigonous female are the general absence of wings (Baker, 1920), and the presence of an ovipositor in certain species (Buckton, 1882, p. 119). Davis (1908) also noted the presence of "sensoria" on the hind tibiae as a secondary sexual character of the amphigonous female, "at least in the subfamilies Pemphiginæ, Schizoneurinae, Lachninae and Aphidinae."² Internally, the most conspicuous features are the presence of a spermatheca and a pair of collateral glands. The accessory glands, as well as the vagina, of which they are an evagination, and also the oviducts, are easily recognizable on account of their relatively thick walls. The large amphigonous eggs and their nurse cells are also very characteristic and are in evidence in the ovaries early in the embryonic stage of the mother. Cleavage and the formation of the blastoderm do not begin until after the eggs are fertilized and deposited. The amphigonous female is oviparous. The eggs are covered with a vitelline membrane and chorion.

GENERAL FEATURES OF PARTHENOGENESIS IN APHIDS.

Among the aphids of temperate countries, aphidologists distinguish between (1) "stem mothers," which are the parthenogenetic individuals hatching from the overwintering amphigonous eggs, and (2) later parthenogenetic generations. The former are typically apterous; the latter, either apterous or alate. In the fall

² The typical genus of Schizoneurinae, which is *Schizoneura* Hartig, 1837, is considered by Baker (1920) as a synonym of *Eriosoma* Leach, 1818. He grouped the latter under the tribe Eriosomatini of the subfamily Eriosomatinae. The subfamily Pemphiginæ has been reduced by the same author to tribe Pemphigini under the subfamily Eriosomatinae; and Lachninae, to Lachnini under Aphidinae.

there is also a third form, the generation of "sexupara," that is, parthenogenetic individuals which give rise to amphigonous forms. These are, as a rule, alate (Patch, 1920). In all specimens of parthenogenetic aphids which I have dissected neither spermatheca nor colleterial glands were found. The absence of these structures was apparently first reported by von Siebold (1839) and subsequently confirmed by other authors. In contrast with the amphigonous forms, the walls of the ovary are uniformly thin and membranous, except at the vagina, where they are somewhat thicker.

Parthenogenetic aphids are viviparous, the entire incubation period being passed within the abdomen of the mother. This is a very unique characteristic, in view of the fact that a similar case does not occur in closely related families. The Phylloxeridæ, which is the only other family with the Aphididæ in the superfamily Aphidoidea, also have parthenogenetic generations, but they are always oviparous. In certain other families of the order Homoptera, like the Aleyrodidæ, parthenogenesis and viviparity are not correlated.

In parthenogenetic aphids, the development of the eggs proceeds in the ovaries long before deposition, eggs in the blastoderm stage having been observed within the abdomen of parthenogenetic embryos. There is no formation of a vitelline membrane and chorion.

MODIFYING FACTORS IN THE PRODUCTION OF AMPHIGONOUS INDIVIDUALS.

As has been suggested elsewhere in the present paper, aphids seem to have the tendency indefinitely to reproduce parthenogenetically under favorable environmental conditions. As experimental evidence favoring this view may be cited Ewing's (1916) work on *Aphis avenæ* Fabricius, in which he found that he could maintain continuous and uninterrupted parthenogenetic reproduction through as many as eighty-seven generations in the material he experimented with on the Pacific Coast of the United States. In that region, oviparous forms in any aphid species had not been known, except in very few cases. His experiments, unfortunately, had to be brought to a close through the dying of all the individuals in his eighty-seventh generation from excessive heat; otherwise, he would probably have been able to observe parthenogenetic reproduc-

tion for a much longer period, if not indefinitely. Earlier investigators, like Bonnet (1745) and Kyber (1815), had previously observed the maintainence of continuous parthenogenetic reproduction in various species of aphids for long periods of time.

Males and oviparous females are known to be produced only under the prolonged influence of extremes of temperature, such as during the winter in temperate climates, and, as certain investigators claim, in cases of scarcity of food. Observations on this modifying action of climate and food, according to Buckton (1882, p. 109) were reported by Bonnet in 1745, and later confirmed by De Geer in 1773.

From our somewhat fragmentary knowledge of tropical aphids, we may tentatively infer, in the absence of more definite evidence to the contrary, that representatives of this family reproduce exclusively by parthenogenesis in warm countries. The following table gives a partial list of the localities in which a continuous parthenogenetic reproduction throughout the year has been observed. It will be noted that the various localities included in the list are characterized either by the total absence of winter or by a relatively mild climate.

LOCALITY	SPECIES	AUTHORITY
France (Orleans)	<i>Aphis rumicis</i> L.	Gaumont (1913)
Germany (Bremen?)	<i>Hyalopterus trirhodus</i> Walk.	Börner (1914)
	<i>Rhopalosiphum lac-</i> <i>tucæ</i> Kalt.	<i>ditto</i>
Holland	<i>Aphis gossypii</i> Glov.	van der Goot (1915)
	<i>Aphis hederæ</i> Kalt.	<i>ditto</i>
	<i>Aphis abietina</i> Walk.	<i>ditto</i>
	<i>Aphis rumicis</i> L.	<i>ditto</i>
	<i>Eriosoma lanigera</i> Hausm.	<i>ditto</i>
	<i>Macrosiphum granarium</i> Kirby	<i>ditto</i>
	<i>Myzus persicæ</i> Sulz.	<i>ditto</i>
India	<i>Aphis brassicæ</i> L.	Maxwell-Lefroy (1907)
	<i>Aphis cardui</i> L. var.	<i>ditto</i>
	<i>Aphis gossypii</i> Glov.	<i>ditto</i>

South Africa	<i>Myzus persicæ</i> Sulz.	Moore (1912)
Sudan	<i>Aphis sorghi</i> Theob.	Vuillet (1914)
Sudan, Anglo-Egyptian	<i>Aphis sorghi</i> Theob.	Theobald (1904)
United States:—		
California	<i>Aphis avenæ</i> Fabr.	Ewing (1916)
	<i>Macrosiphum rosæ</i> Ream.	Russell (1914)
Florida	<i>Aphis brassicæ</i> L.	Quaintance (Herrick, 1911)
Indiana ³	<i>Macrosiphum granarium</i> Kirby	Phillips (1916)
Texas	<i>Aphis pseudobrassicæ</i> Davis	Paddock (1915)
Virginia ³	<i>Macrosiphum granarium</i> Kirby	Phillips (1916)
South Carolina	<i>Callipterus trifolii</i> Monell	Davis (1914)
Southern U. S. ⁴	<i>Toxoptera graminum</i> Rond.	Webster and Phillips (1912)
Washington	<i>Pemphigus betæ</i> Doane	Doane (1900)

Supplementary to the above data may be cited here the other paper of van der Goot (1917, p. 2), who, after three years of biological and taxonomic work on the Aphididæ in Java, reported that he had never found amphigonous individuals in that country—not even at high mountain elevations where the temperature falls to the freezing point at night. Likewise, several years of casual observation and collecting in the Philippine Islands by me failed to disclose the male and oviparous-female forms. So far as I am aware, the occurrence of amphigonous aphid individuals in any other tropical country has not been definitely reported. It should be borne in mind, however, that failure to discover such forms in a given locality does not prove their non-existence there; although, when workers carrying on investigation for years in tropical regions report their inability to find amphigonous forms in any season of the year, there is some ground for suspicion that partheno-

³ Amphigonous individuals and winter eggs of that species also found in this locality.

⁴ South of the 35th parallel.

genetic reproduction is continuous and uninterrupted, at least among the more common species of tropical aphids. If such a condition does obtain, the most reasonable explanation appears to be that in the tropics conditions are relatively more uniformly favorable to the aphids, both with respect to the climate and the nutritive factors in the environment.

Patch (1920), on the other hand, in a very interesting general treatise on the life cycle of aphids, remarks that "in tropical climates experiencing a wet and a dry season gamogenetic [amphigogenous] eggs are produced to tide over the period of famine"; but unfortunately she does not cite any specific evidence or authority to support her thesis. It is not improbable, however, that some rare cases of amphigonous forms might occur in those tropical countries where, as she suggests, the year is divided between a wet and a dry season,⁵ in view of the fact that in the height of the

⁵ Such a condition obtains in the Philippine Islands, Java, and many other countries of the tropics of both hemispheres.

hot, dry season, when conditions are less favorable for many living organisms, certain species of insects are known to assume a resting state, presumably corresponding to hibernation in temperate climates.

In temperate countries, as a rule, reproduction of aphids by parthenogenesis is continuous during the milder seasons of the year, and amphigonous forms do not appear until the onset of the fall, when the low temperatures begin to affect the insects unfavorably. Exceptions to this generality are determined by the modification of the climate in a given region through the agency of various factors, such, for instance, as the prevailing winds blowing from the ocean and causing the summers to be "more moderate and the winters milder" on the Pacific Coast of the United States than in regions situated at similar latitudes in the interior and on the Eastern Coast.⁶ The aphids in the former locality are thus subjected to comparatively more favorable conditions throughout the year and, consequently, they rarely, if ever, undergo heterogony (Ewing, 1916, and Swain, 1919, p. 8).

⁶ R. DeC. Ward. 1918. *Climate Considered Especially in Relation to Man*, second edition, revised: 44. xvi+380 pp. G. Putnam's Sons, New York and London.

THE NATURE OF INFLUENCE OF EXTREMES OF TEMPERATURE AND
LESSENING OF FOOD SUPPLY IN THE DETERMINATION OF
AMPHIGONY.

It may be inferred from the foregoing considerations that winter, with its attendant low temperatures and inadequate food supply, plays a very important, if not an exclusive, part in the determination of amphigony. Amphigony correspondingly becomes of less frequent occurrence as winter becomes less severe in a locality, until in tropical regions where the temperature and, incidentally, the food supply also are more equably maintained throughout the year, amphigony occurs very rarely, if at all.

In this connection, it is interesting to note that, although heterogony has been brought about evidently as an adaptation to unfavorable environmental factors, the effects of low temperatures do not seem to be a necessary immediate stimulus in the production of amphigony and that aphid strains normally undergoing heterogony may continue to produce an amphigony generation and lay eggs at least in the fall following the spring of the same year in which the insects from the open are taken into the greenhouse. The following experimental evidence, which has led me tentatively to arrive at this conclusion, is based on preliminary observations, which will have to be confirmed by further investigations under more adequate control:

In July, 1920, seedlings of *Tanacetum vulgare* Linnæus were transferred to the greenhouse of the Bussey Institution. At about the middle of August, after the plants had been well started, they were inoculated with their common aphid pest, *Macrosiphum tanacetii* Linnæus. The host plants appeared to grow normally and the aphids continually reproduced parthenogenetically until about the end of October, 1920. In October the temperature outdoors began to fall every now and then, especially at night, and at this time the greenhouse was kept heated to an average of about 65°F. This temperature had been observed previously by Ewing (1916) to be the optimum for aphids, in that it is least stimulating to the production of wings in the viviparous forms; and this behavior may be interpreted as an indication that the insects were under more favorable environmental conditions than the individuals which showed greater tendency to produce wings when subjected to other

temperatures. In spite of the precautions observed in the present experiments, at about the end of October and the first week of November, 1920, when the tansy plants were still in apparently good condition, the aphids produced amphigonous individuals and laid winter eggs, in the same manner as the insects of identical species which were exposed to the more adverse weather conditions in their natural environment outdoors.

In the same greenhouse were a number of plants of *Nicotiana glauca* Otto et Fink. These had been observed by me since September, 1919, to be infested with *Myzus persicae* Sulzer. The insects, which are a common greenhouse pest in this part of the country, were probably descendants of parents that had been associated with greenhouse plants for a long period of time, and thus had been continually protected for generations from the drastic effects of winter. These individuals of *Myzus persicae* in the greenhouse, which were under the influence of the same temperature conditions as the tansy aphids, continuously reproduced parthenogenetically throughout the winter of 1919-1920 and of 1920-1921.

At the time the above experiments were conducted, there was no facility available for a more accurate regulation of temperature and other conditions. The simultaneous presence in the same place of parthenogenetic forms of *Myzus persicae*, however, tends to eliminate to some extent the possibility of adverse conditions existing in the greenhouse and bringing about amphigony in *Macrosiphum tanacetii*. Another difficulty in the present experiments was that I had no opportunity to work with material of identical species for control. However, under natural conditions outdoors in this locality, both *Myzus persicae* and *Macrosiphum tanacetii* begin to produce winter eggs at about the same time of the year, in the fall.

In apparent contradiction to my findings on *Macrosiphum tanacetii* are the results reported by Slingerland (1893) in his work on *Myzus achyrantes* Monell, which species is considered by Gillette and Taylor (1908) as a synonym of *M. persicae*. On April 2, 1890, Slingerland isolated the nymph of a wingless, parthenogenetic female, and within two years and ten months from that date he succeeded in raising from his material sixty-two successive generations of parthenogenetic individuals. The work was done

at the Cornell Agricultural Experiment Station, at which locality winter is more or less severe, and this species is known, under natural conditions, to undergo an alternation of generations during the year. It should be noted, however, that *Myzus achyranthes* is a common pest of the greenhouses in Ithaca, as Slingerland himself admits in his paper. It is highly probable, although he does not specifically say so, that he obtained his material of this species from stock which had been in existence in the greenhouse for generations, and, as was the case with *Myzus persicæ* in the present experiments, the progenitors of the nymph with which he started his cultures might have come from a strain that had been reproducing exclusively by parthenogenesis as a result of prolonged seclusion from the untoward effects of winter. Under these circumstances then, Slingerland's results would tend to corroborate mine, instead of contradicting them. Nor would Ewing's (1916) eighty-seven continuous parthenogenetic generations of *Aphis avenæ* disprove my results, in view of the fact that the source of his material was the Pacific Coast of the United States, where this aphid has been known to reproduce normally by parthenogenesis for indefinite periods. This author himself states in his paper that he was unable to find amphigonous forms of the species outdoors during the entire time that his experiments were in progress. The results reported by earlier investigators, like Bonnet (1745) in France, on nineteen continuous parthenogenetic generations of *Aphis sambuci* Linnæus, and Kyber (1815) in Germany on parthenogenetic reproduction during a four-year period by *Macrosiphum rosæ* Linnæus (= *Siphonophora rosæ* Koch) and *Myzus persicæ* Sulzer (= *Rhopalosiphum dianthi* Schrank), may have to be classed in the same category as Ewing's or Slingerland's, for the reason that (1) at least one species, *Myzus persicæ*, as I have stated, is a common greenhouse pest, and (2) the material with which they worked might have come from stocks which, in their respective localities, had been reproducing outdoors normally by parthenogenesis throughout the year, cases of which have been reported lately from both countries (Gaumont, 1913, and Börner, 1914). In this event, their results would not tend to contradict mine.

It would not be safe, on the basis of the foregoing evidence, to

formulate definite conclusions. The present observations, however, suggest the following preliminary deductions:

1. Heterogony in certain aphids of temperate climates has probably become a rhythmic process, occurring regularly at definite periods in their yearly cycle of generations and independently, for a period at least, of the immediate stimulus brought about by adverse temperature conditions.

2. Amphigonous reproduction in these aphids, although evidently maintained as an adaptation to, and under the influence of adverse climatic conditions, continues to occur at these definite cyclical intervals for some time after the causative factors have been removed.

The foregoing views find additional support in the fact that in nature in temperate climates amphigonous and parthenogenetic individuals of identical species in the same locality and feeding on the same parts of a host plant live side by side for considerable periods of time, even weeks, on the onset of the fall. I have noticed such a condition in Boston, and other workers have observed it elsewhere. This failure of all the individuals to respond simultaneously in the same manner to a given condition of the environment tends to show that environmental factors do not furnish the immediate or adequate stimulus in the determination of amphigony.

In 1907 Tannreuther (1907), in a paper on *Melanoxanthus salicis* Weed, *M. salicicola* Thomas, and several other species of aphids, announced somewhat similar views. He said in part that "external conditions, whether severe or normal, would not bring about the production of sexual generation before a definite number of parthenogenetic generations had intervened." He further noted, after two seasons of experimentation, that "if a stem mother and offspring were kept in favorable conditions in the greenhouse on the same species of hosts as out of doors, the time and length of period for each succeeding generation was approximately the same as out of doors, and that in both instances the sexual females and males appeared after the intervention of six parthenogenetic generations."

It may be necessary, at this juncture, to call particular attention to the fact that in the foregoing discussion the rôle of temperature in influencing the form of aphid reproduction is by no

means belittled. As has been stated above, adverse temperature conditions evidently play a very important part in the determination of amphigony, and a uniformly mild temperature is apparently conducive to an indefinite maintenance of parthenogenetic reproduction. The point suggested, however, is that the effect of continuous subjection of an aphid strain which normally undergoes heterogony to mild temperature does not immediately become manifest. But this fact does not preclude the possibility that the cumulative effects on more than one yearly cycle of generations might bring about a change in the method of reproduction to one of continuous parthenogenesis. I have no data bearing on the reaction of the greenhouse aphids which reproduce continuously by parthenogenesis to the adverse weather conditions outdoors during the fall and winter months.

I am not prepared to discuss from personal observations the relation between scarcity of food and the determination of amphigony. There is apparently nothing in the literature which touches this subject, except the statement of Tannreuther (1907) that "abundance or scarcity of food is not a factor in determining the sex in the case of the aphids," for which, however, he presents no concrete experimental evidence. Of some possible interest in connection with this problem are the experiments by Gregory (1917), who found that by subjecting parthenogenetic individuals of *Macrosiphum pisi* Kalténbach (= *M. destructor* Johnson) to varying periods of starvation, in certain cases carrying her experiments to the maximum possible points without killing the insects, she could induce the production from apterous mothers of alate offspring, which, as shown by her check cultures, would otherwise have been apterous. It is, however, apparent from her paper, although she does not state it, that the subsequent offspring of these starved aphids were invariably parthenogenetic and that the production of amphigonous individuals was not artificially induced by the treatment. It is to be regretted that she did not carry her experiments through the succeeding generations after the mother; and the question now arises as to whether the production of amphigonous individuals is induced only by the successive and cumulative effects of starvation on several generations of parthenogenetic individuals. One point is suggested by these experiments, and that is that, as

in the case of temperature conditions, if the quantity of available food has any tendency at all to change the method of reproduction in aphids, the effect does not become apparent immediately. This question, however, needs further investigation before very definite conclusions can be reached.

SUMMARY.

1. The sexual type of reproduction is the only one known to occur in the Aphididæ. This process takes three forms in this family: (a) amphigony; (b) parthenogenesis; and (c) pædogenesis.

2. Amphigony is considered as the more primitive method in insects. Parthenogenesis has practically supplanted it in aphid reproduction.

3. Parthenogenesis in aphids is apparently continuous and uninterrupted under favorable environmental conditions, amphigony occurring only under the influence of low temperatures and, as certain authors claim, inadequate food supply.

4. Aphids in tropical and other warm climates appear to have the tendency to reproduce exclusively by parthenogenesis. The same condition apparently obtains among greenhouse aphids in temperate climates.

5. Aphids in colder climates undergo heterogony as an adaptation to adverse environmental conditions. In certain species, the appearance of the amphigonous generation seems to be a rhythmic process, which continues to occur at definite cyclical intervals for some-time after the influence of low temperature has been eliminated.

6. Nothing very definite is known about the relation of food and heterogony. If the quantity of food has any influence at all on the determination of amphigony in a parthenogenetic mother, the effect does not become manifest in the immediate offspring.

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